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Regional disparity in the axial skeleton of Saurichthyidae and implications for axial regionalization in non-teleostean actinopterygians

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Keywords
Saurichthyidae; *Birgeria*; Actinopterygii; vertebral column; morphology; evolution; axial skeleton; Triassic.

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Abstract

The postcranial axial skeleton of actinopterygian fishes is typically divided into three regions: (1) an anterior abdominal region, (2) a posterior caudal region and (3) those vertebrae supporting the caudal fin. However, in some actinopterygians, the axial skeleton is more finely subdivided, with up to six morphologically distinct sub-regions recognized. Phylogenetic continuity and homology of structures across these sub-regions have not been investigated in detail, either between or among groups. We examine variation in axial regionalization in saurichthyid fishes, a clade of extinct non-teleostean actinopterygians with highly variable axial skeletal morphology but an otherwise conservative body plan, and compare these findings to other non-teleostean actinopterygians to assess conservation of a regionalized axial skeleton within bony fishes. We document up to eight distinct regions in the vertebral column of Triassic *Saurichthys*: (1) a postoccipital region, (2) an anterior and (3) a posterior abdominal region, (4) a transitional region spanning the abdominal–caudal boundary, (5) an anterior and (6) a posterior caudal region and (7) preural and (8) ural regions. Based on taphonomical and morphological evidence, the transitional region appears to function in axial stiffening in the area of the median fins, whereas the abdominal region is highly flexible. The degree to which these axial regions are osteologically differentiated is highly variable across Saurichthyidae, implying iterative evolution of differentiation and de-differentiation over relatively short geological timescales. Such variably expressed regionalization was also identified in the outgroup non-teleostean actinopterygians *Birgeria* and *Australosomus*. Despite variation in morphological disparity, the regions identified in saurichthyids correlate well with those documented in some teleosts and Paleozoic actinopterygians, suggesting potential deep patterning homology but independent evolution of specific regionalized axial morphologies in response to changing functional demands.

Introduction

A highly regionalized axial skeleton consisting of cervical, thoracic, lumbar, sacral and caudal regions has historically been viewed as a typical feature of tetrapods (Sallan, 2012). Although best-developed in mammals, these regions can be morphometrically recovered even within groups showing more subtle variation along the vertebral column (e.g. snakes: Head & Polly, 2015; odontocete cetaceans: Buchholtz & Gee, 2017); this is referred to as 'regionalized but de-differentiated' (Buchholtz and Gee, 2017). In contrast, the vertebral column of actinopterygian fishes has been divided into only two general areas: an abdominal and a caudal region, distinguished by the presence of haemal spines in the latter (e.g. Bird & Mabee, 2003). Some actinopterygians show more complex patterns of axial regionalization (e.g. the Weberian vertebrae of ostariophysans in the anterior column; the ural skeleton of teleosts: Bird and Mabee, 2003), but historically these have been interpreted as isolated specializations of specific lineages of highly derived teleosteans, external to a conserved framework of axial patterning. However, detailed examination of the axial skeleton in the Paleozoic (Carboniferous) basal actinopterygian *Tarrasius* indicates five clearly differentiated regions within the precaudal axial skeleton (Sallan, 2012), and more recently five

distinct axial regions have been recognized in salmonids (De Clercq *et al*., 2017), which have a generalized body plan. These reports raise intriguing questions as to the prevalence of axial regionalization in actinopterygians and structural variability within morphologically disparate regions.

In vertebrates, precaudal axial regionalization is patterned by spatially and temporally collinear expression of *Hox* genes within the somitic mesoderm during embryonic development (Burke *et al*., 1995). Gene expression in zebrafish, the best-known actinopterygian developmental model system, suggests anteriorly shifted, overlapping patterns of Hox expression during embryonic development (Prince *et al*., 1998; Morin-Kensicki, Melancon & Eisen, 2002). Sharks, on the other hand, show a regionalized Hox expression pattern more similar to tetrapods, although the axial regions are effectively anatomically undifferentiated (sensu Buchholtz and Gee, 2017), leading to the hypothesis that an anteriorized pattern may be derived within Actinopterygii (Oulion *et al*., 2011). The question arises as to when within Actinopterygii this anteriorized axial morphology arose, how widespread tetrapod-like regionalization is within non-teleost actinopterygians, and whether the caudal skeleton also shows conserved patterns of regionalization.

The predominantly Early Mesozoic saurichthyids are a speciose group (over 50 species) of non-teleostean actinopterygians characterized by an elongated body and posterior displacement of the dorsal and anal fins. Phylogenetically, Saurichthyidae + *Birgeria* are positioned as sister-group to crown actinopterygians (Argyriou *et al*., 2018). Elongation in Saurichthyidae has been correlated with increasing numbers of abdominal vertebrae (Maxwell & Wilson, 2013), and body size also affects vertebral counts in the clade (pleomerism; Wu, Sun & Fang, 2018). Extensive morphological variation has been reported in the anterior caudal region of saurichthyids (Wu *et al*., 2015), but changes in regionalization along the length of the vertebral column have never been comprehensively investigated. Convergent evolutionary reductions in the squamation combined with qualitative disparity between regions of the vertebral column (e.g. Maxwell *et al*., 2015) make saurichthyids an ideal group in which to investigate regionalization in non-teleostean actinopterygians.

Institutional abbreviations

PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Materials and methods

Terminology and general axial anatomy in Saurichthyidae

Many terms, some group-specific or with different meanings ascribed by different authors, have developed for structures associated with the actinopterygian vertebral column. These are clarified in Table 1; *Saurichthys*-specific details are discussed below to help orient the reader. As with many non-teleostean actinopterygians, the vertebral column of Saurichthyidae is characterized by an unconstricted notochord; ossified centra are absent (aspondylous vertebrae: Arratia, Schultze & Casciotta, 2001). Within one axial segment, ossified components dorsal to the notochord include neural arches with medially unfused neural spines; the neural arches articulate with adjacent arcual elements via zygapophyses (Stensiö, 1925). Posterior to the true neural arch of each segment, *Saurichthys* possesses a second neural arch-like element, convergent in morphology to the first but homologous to an expanded interdorsal element (Maxwell, Furrer & Sánchez-Villagra, 2013). Supraneurals are absent, as are ossified ribs and intermuscular elements. Ossifications ventral to the notochord are more variable, but when present, these consist of an anterior element (ventral arcocentrum/haemal arch) and a posterior element, the interventral (Stensiö, 1925). As with the neural arches, the haemal processes are not medially fused. The term 'haemal spine' has been used in the literature to refer to these ventrally extended haemal arches in *Saurichthys* (Rieppel, 1985; Wu *et al*., 2015); here, we refer to these structures as haemal processes sensu Nielsen (1942), and restrict use of the term haemal spine to refer exclusively to a median structure that develops by extension of the haemal arches (Table 1). The caudal fin skeleton of saurichthyids is abbreviated diphycercal (e.g. Rieppel, 1985).

We use the axial anatomy of the phylogenetically basal Middle Triassic species *Saurichthys rieppeli* Maxwell *et al*., 2015 (PIMUZ T 61) as a template of regional variation across Saurichthyidae. The axial skeleton of this specimen is superbly preserved, and this species shows the maximum observed degree of regionalization, allowing comparison to other saurichthyids and outgroups. For these comparisons, we personally examined specimens of Saurichthyidae and *Birgeria* in the collections of the SMNS and PIMUZ, with reference to the literature (Table S1).

Regions were identified based on overall morphological disparity and comparison with previous studies on actinopterygians (Morin-Kensicki *et al*., 2002; Sallan, 2012; De Clercq *et al*., 2017; see discussion for a critical evaluation). While this approach is more subjective than morphometric approaches (Head and Polly, 2015; Buchholtz & Gee, 2017), it provides a baseline against which to test quantitatively derived hypotheses of regionalization. Moreover, morphometric methods cannot easily be applied to taxa with aspondylous vertebrae, which include many extinct non-teleostean actinopterygians occupying key phylogenetic positions.

Results

Regionalization in *Saurichthys rieppeli*

The following eight regions are differentiated (or hypothesized to be distinct, in the case of Region I) in the axial skeleton of PIMUZ T 61 (Figs. 1 and 2a):

(1) Postoccipital region ('cervical' sensu Morin-Kensicki *et al*., 2002): The anteriormost vertebrae are obscured by overlying elements in *Saurichthys rieppeli*, making the presence of a differentiated 'cervical' region difficult to assess. The presence of this region is inferred based on related taxa (Fig. 2b).

Table 1 Clarification of anatomical terminology used in the text. Not all listed structures are present in all taxa

Term	Definition	Reference
Arcocentrum	Ossification of cartilage extending from the arcualia around the notochord	Schultze & Arratia, 1986
Arcualia	Basidorsal and basiventral cartilages, precursors of the neural and haemal arches	Gadow & Abbott, 1895
Interdorsal/Interventral	Usually small elements posterior to and sometimes fusing with the neural and haemal arches. In saurichthyids, they may develop into a second neural/haemal arch	Gadow & Abbott, 1895; Stensiö, 1925
Haemal arch	Ventral ossification of the basiventral arcual forming the lateral wall of the haemal canal	Gadow & Abbott, 1895
Haemal process	Posteroventral elongation of the haemal arch; paired. Associated with the abdominal–caudal transition, similar to 'true' haemal spines	Nielsen, 1942
Haemal spine	Extension of the haemal arches ventral to the haemal canal; always median	Grande & Bemis, 1998
Infrahaemal	Independent median ventral ossification articulating with the haemal arches	Nielsen, 1942
Neural arch	Ossification of the basidorsal arcual forming the lateral wall of the neural canal	Gadow & Abbott, 1895
Neural spine	Develops as an extension of the neural arches dorsal to the neural canal; may be paired or median	Grande & Bemis, 1998; Arratia *et al.*, 2001
Paraneural plates	Lateral extensions of the neural arches	Wu *et al.*, 2018
Parapophysis	Process for articulation with the ribs derived from the lateral basiventral arcual; migrate ventrally and may coalesce with the ventral basiventral arcual derivatives posteriorly	Goodrich, 1930; De Clercq *et al.*, 2017
Supraneural	Median ossification articulating with the neural spines	Arratia *et al.*, 2001
Zygapophyses	Paired anteriorly directed processes (prezygapophyses) of a neural or haemal arch, articulating with the posteriorly directed processes (postzygapophyses) of the preceding arch. Refers to functionally similar non-homologous structures within Vertebrata.	Stensiö, 1925; Schaeffer, 1967; Bird & Mabee, 2003; Sallan, 2012

(2) Anterior abdominal region (Figs. 1 and 2a). The neural spine and its segmental duplicate are only gently posteriorly inclined and dorsally expanded. Zygapophyses are well developed with a small secondary dorsal projection anterior to the neural spine (Fig. 1a). The most anterior preserved 11–12 segments in *S. rieppeli* are morphologically differentiated from more posterior segments by the presence of a triangular ventral ossification positioned between the neural arch and its duplicate. These ossifications are largest anteriorly, and become smaller posteriorly. There are two possible interpretations for the ventral ossifications: paraneural plates ossified along the horizontal septum following Wu *et al*. (2018) based on *Saurichthys spinosa* and interpreted as a functional adaptation for axial stiffening, or parapophyses associated with cartilaginous ribs. Unlike paraneural plates, which co-ossify with the neural arch (Wu *et al*., 2018), the elements in *S. rieppeli* lie ventral to the neural arches and ossify independently. This pattern is identical to that seen in the ossified parapophyses in Acipenseriformes (Leprévost *et al*., 2017: fig. 3F); thus, in *S. rieppeli* we find parapophyses to be the more plausible interpretation for these ventral elements.

(3) Mid-abdominal region (Fig. 1b). The mid-abdominal region, characterized by the absence of ossified parapophyses, begins posterior to segment 12. A second change occurs within this region: around segment 20, the mid-abdominal neural spines become narrower and more posteriorly inclined, and the dorsal expansion of the prezygapophysis is lost. This does not correlate with a change in ventral ossifications. Based on broader taxonomic comparisons within saurichthyids, the ventral ossifications appear to better reflect regional variation in the anterior column (regions II–III).

(4) Transitional region (Figs. 1c and 2a). This region spans the abdominal–caudal transition, and can be subdivided into three parts (IVa–c). In the region of the pelvic fins, paired ventral ossifications, here identified as haemal arches forming ventral arcocentra and fused with ossified interventrals, reappear and rapidly become stereotypically spool-shaped (Region IVa). Each ventral element spans one axial segment with a foramen in the posterior half interpreted as transmitting the intersegmental vessels (Stensiö, 1925). Immediately anterior to the anal fin, long posteriorly directed processes are present (Region IVb), originating from the posterior half of a ventral arcocentrum ventral to the vascular foramen, and identified as haemal processes. The right and left haemal processes are unfused. Posteriorly, the ventral arcocentra become progressively more weakly ossified, and the differentiated haemal arch and interventral components cease to fuse to each other (Region IVc).

(5) Anterior caudal region (Fig. 1d and 2a). Around the midpoint of the anal fin base, the haemal processes are reduced, and by the end of the anal fin base no mineralized ventral elements are present. Also at around the midpoint of the dorsal fin base, the neural spines rapidly reduce in size until no longer present, while the

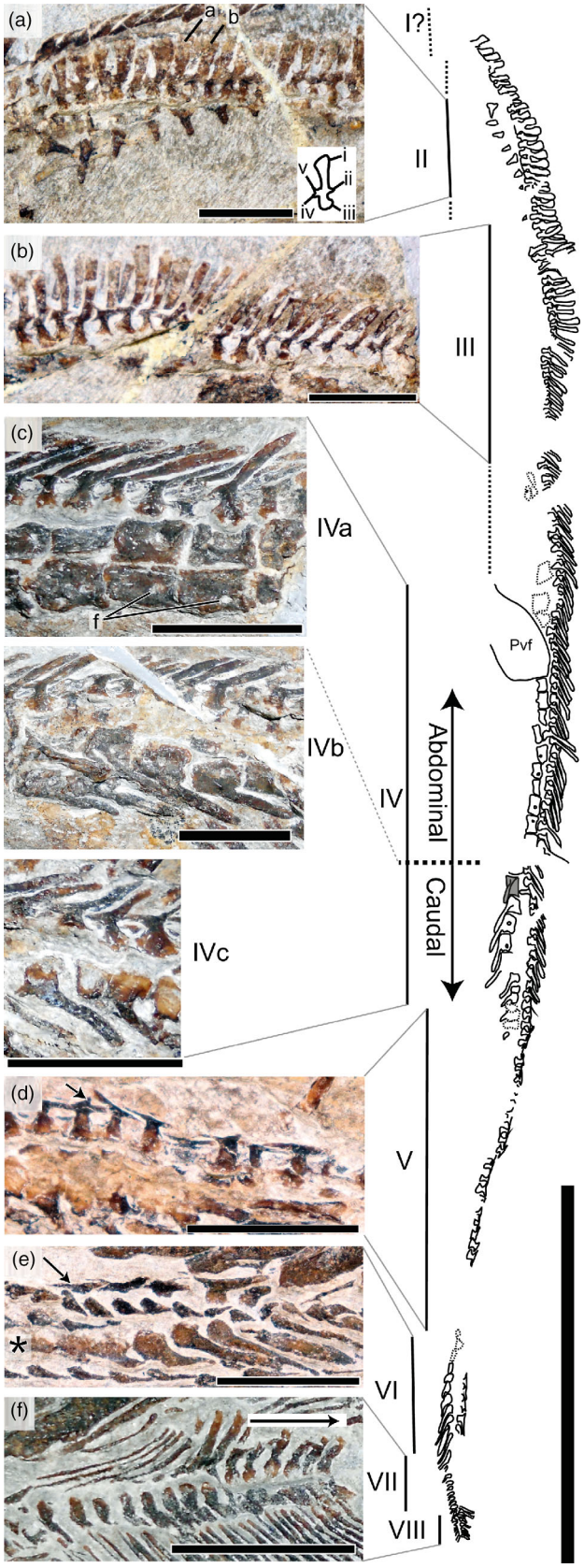

Figure 1 *Saurichthys rieppeli* (PIMUZ T 61) illustrating regions as described in the text. (a) anterior abdominal region (II), inset illustrates a neural arch. i, neural spine, ii, postzygapophysis, iii, pedicle of neural arch, iv, prezygapophysis, v, dorsal expansion of prezygapophysis. (b) mid-abdominal region (III); (c) transitional region (IV), note that in IVa the contralateral ventral elements are preserved in articulation in ventral view; (d) caudal region (V); arrow indicates neural arch with transitional morphology; (e) peduncle region (VI), arrow indicates row of neural arches; asterisk indicates row of haemal processes, the intervening row is a scale row; (f) caudal fin region (VII–VIII), arrow above inferred preural–ural transition. Abbreviations: a, 'true' neural arch; b, duplicated neural arch (interdorsal); f, foramina for intersegmental vessel; Pvf, pelvic fin. Scale bar = 10 mm (a–f), 100 mm (overview).

zygapophyses remain present, resulting in T-shaped neural arches.

(6) Peduncle region (Fig. 1e). Immediately anterior to the caudal fin, co-ossified ventral arcocentra and haemal processes reappear. The anteriormost two elements consist only of the ventral arcocentra. Unlike in regions III–IV, a haemal arch is present for every neural arch. Haemal processes are oriented parallel to the notochord in the peduncle region. Neural spines, oriented approximately parallel to the notochord, also reappear in this region.

(7) Preural caudal region (Figs. 1f and 2c). Dorsal and ventral elements in the caudal fin are oriented vertically and support lepidotrichia. The ventral elements are relatively thick and show a constriction between the haemal arch and spine (the paired nature of this structure is unclear), indicating that these are preural. The preural and ural regions are differentiated by the absence of a haemal arch in the latter (Nybelin, 1963).

(8) Ural region (Figs. 1f and 2c). Although not well-preserved, there appears to be a morphological change part way along the fin, which we interpret as the approximate location of the preural/ural boundary. The ventral elements (hypurals) become flattened and lose the constriction between arch and spine, and the dorsal elements become smaller. Although disruption of the terminal lobe prevents an exact count, *S. rieppeli* has at least six hypurals, making the caudal skeleton polyural, as is typical of non-teleost actinopterygians (Schultze & Arratia, 1989).

Regionalization across Saurichthyidae

There is extensive variability in the axial skeleton of saurichthyids. We provide a brief overview of differences in regionalization between taxa to understand trends and variability within the clade (Fig. 3; Table S1).

Early Triassic saurichthyids

As far as has been described, there is little difference in axial regionalization between *Saurichthys rieppeli* and phylogenetically basal/phylogenetically indeterminate Early Triassic saurichthyids (e.g. Kogan & Romano, 2016a, 2016b).

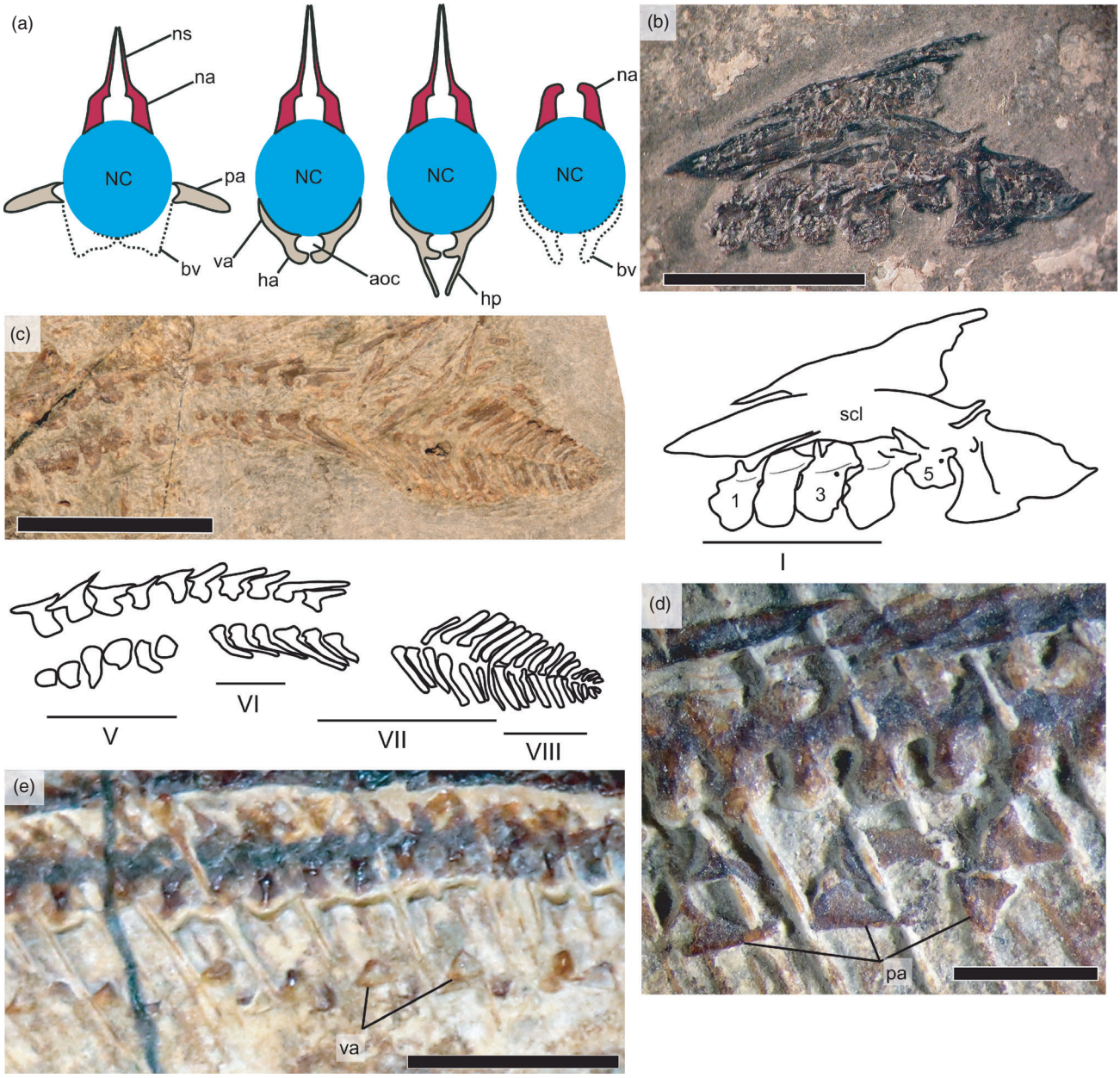

Figure 2 Regionalization across Saurichthyidae. (a) Generalized reconstruction of selected vertebral regions in anterior view, based on *Saurichthys rieppeli*; zygapophyses have been omitted for clarity. The shape of the basiventral cartilages is hypothetical, based loosely on the morphology in *Acipenser* (Hilton, Grande & Bemis, 2011). From left to right: Regions II, IVa, IVb, V. (b) Postoccipital neural arches (Region I) of *Saurorhynchus hauffi* (SMNS 50924; mirrored) preserved in medial view showing short, squat elements and absence of neural spines. Numbers indicate 'true' neural arches. (c) Caudal region of *Saurichthys* (*Costasaurichthys*) *costasquamosus* (PIMUZ T 1275; mirrored) without overlying lepidotrichia, illustrating Regions V, VI, VII, and VIII. (d, e) *Saurichthys* (*Costasaurichthys*) *paucitrichus* (PIMUZ T 59) abdominal region, illustrating the differentiation between parapophyses in Region II (d) and ventral arcocentra in Region III (e). Anterior is to the left in all figure parts. Abbreviations: aoc, aortic canal; bv, basiventral; ha, haemal arch; hp, haemal process; na, neural arch; NC, notochord; ns, neural spine; pa, parapophyses; scl, supracleithrum; va, ventral arcocentrum. Scale bar = 5 mm (b, e); 20 mm (c–d).

One key difference is the much shorter anterior transitional region (IVa) in *S. madagascariensis* than in *S. rieppeli*. This region appears approximately dorsal to the location of the pelvic girdle in both taxa, independent of the end of the body cavity. Differentiated Regions I–II and VI–VIII have not been documented in *S. madagascariensis*, but these regions are not well-exposed in any Early Triassic saurichthyid.

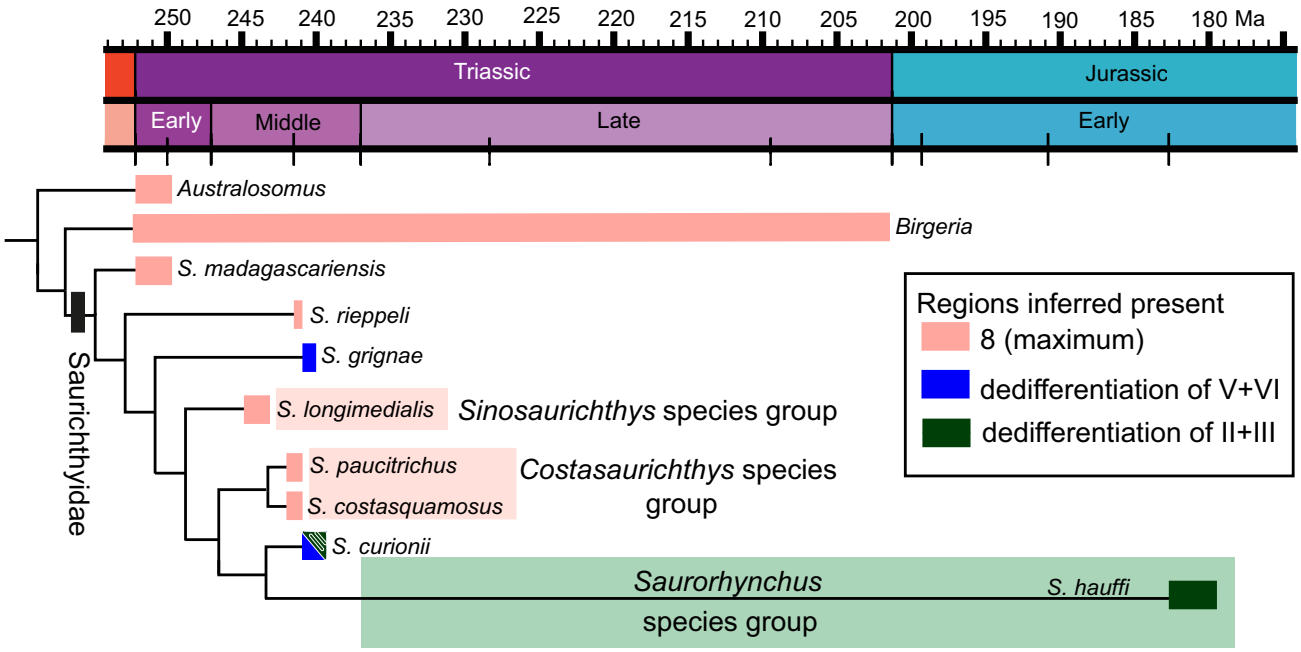

Figure 3 Time-calibrated phylogeny of Saurichthyidae and outgroups modified from Maxwell *et al.* (2015), highlighting repeated occurrences of axial dedifferentiation. Hatching indicates intraspecific variability in differentiation between anterior and posterior abdominal regions in *Saurichthys curionii*.

Sinosaurichthys species group (sensu Tintori, 2013)

In *Sinosaurichthys longimedialis* (Anisian), Region II is characterized by ossified parapophyses; these are replaced by ossified ventral arcocentra in Region III. Region IV is divided into a short anterior region, characterized by very short haemal processes (IVa) interspersed with ossified interventrals, and a longer posterior region (IVb), characterized by alternating haemal processes and interventrals. Region V is differentiated by the loss of haemal processes and neural spines (T-shaped neural arches; Wu *et al.*, 2011). In Region VI, haemal processes reappear, but differentiation of Regions V and VI is relatively weak in this clade.

Saurichthys grignae

This Middle Triassic (Ladinian) species is phylogenetically basal to the better-defined clades higher up the tree (Fig. 3; Maxwell *et al.*, 2015). Region IV lacks subdivisions, and is differentiated from Region V by a change in the orientation of the neural spines and haemal processes (Tintori, 2013). Regions V and VI are not differentiated: since neural spines and haemal processes are not lost in the anterior caudal region, the whole preural caudal region is superficially similar to Region VI of *S. rieppeli*.

Costasaurichthys species group (sensu Tintori, 2013)

The pattern in *Saurichthys* (*Costasaurichthys*) *paucitrichus* (PIMUZ T 59) roughly corresponds to that described for *S. rieppeli*. In particular, Region II is differentiated by ossified parapophyses in a 1:2 relationship with the neural arches (described by Rieppel, 1992 as haemal arches). These have an elongated morphology (Fig. 2d) and are ossified on both the dorsal and ventral surfaces, but around segment 10 become small, nodular and are ossified on only one surface (Fig. 2e). We interpret this shift as a change from ossified parapophyses, characterizing Region II, to ossified ventral arcocentra, characterizing Region III. Haemal processes appear dorsal to the anal loop, and are equal in number to the neural arches (Region IV). The first haemal process is not fused with the ventral arcocentrum (IVa), but more posteriorly the two elements are co-ossified (IVb). The anteriormost haemal processes are bifid, but towards the posterior end of the anal fin the processes become unbranched (IVc). This point roughly corresponds to the appearance of T-shaped neural arches, although these have a transitional morphology until the posterior end of the dorsal fin. Posterior to the anal fin, the haemal processes gradually become smaller and disappear. We interpret this as a gradual transition between Regions IV and V, rather than a sudden shift to a caudal morphology as documented in *S. rieppeli*.

The regionalization pattern of *Saurichthys* (*Costasaurichthys*) *costasquamosus* is similar to *S. paucitrichus* but provides additional information on caudal regionalization (PIMUZ T 1275; Fig. 2c). In this species, regions V–VIII are differentiated. The preural–ural transition is not entirely clear, but at minimum seven hypurals are present.

Saurichthys curionii

Regions II and III are differentiated by the presence of ossified parapophyses in the former; however, differentiation of these

regions is not present in all specimens, even within a given maturity class– namely, gravid females. A single specimen (PIMUZ T 3917) shows structures that we interpret as atypically ossified ribs in region II. Region IV is differentiated by ossified haemal arches in a 1:1 relationship with the neural arches, and begins well anterior to the pelvic girdle; haemal processes occur posterior to the pelvic girdle (IVb). The transition from Region IV to V ventral to the dorsal fin is characterized by a sudden change in the angle of the neural spines (Rieppel, 1985); the haemal processes become much shorter and thinner at this point. Although the haemal processes are slightly more robust in the caudal peduncle, this transition is gradual and subtle.

Saurorhynchus species group (sensu Maxwell *et al.*, 2015)

Detailed data for this clade is only available for *Saurorhynchus hauffi* (Early Jurassic; Maxwell & Stumpf, 2017). Region I consists of ~4 neural arch-like elements, and is differentiated from Region II by the block-like shape of the centra and the relative reduction of the prezygapophyses and neural spines (Fig. 2b). Regions II and III are not differentiated. There are two subregions within Region IV; the anteriormost (IVa) consists of short haemal processes, which gradually lengthen, and the second (IVb) is characterized by elongation and distal bifurcation of the neural spines and haemal processes anterior to and supporting the dorsal and anal fin, respectively. Posterior to the median fins, the neural spines and haemal processes become laterally expanded (V), as described in *Saurichthys grignae* (Tintori, 2013), and cease to bifurcate. In Region VI, bifurcation resumes and the notochord becomes very narrow. The dorsal and ventral elements in Region VII are in articulation with each other, and there is a change in the angle of the neural and haemal arches.

Regionalization in outgroups: *Birgeria*

The Triassic actinopterygian *Birgeria* is hypothesized to be the sister-group of Saurichthyidae, whereas the Early Triassic *Australosomus* falls basal to this clade on the neopterygian stem (Fig. 3; Argyriou *et al.*, 2018). Thus, both taxa are informative in understanding the evolution of regionalization in Saurichthyidae.

As in saurichthyids, the vertebral column of *Birgeria* is aspondylous, consisting of ossifications dorsal and ventral to the notochord. Although previous studies did not recognize regional disparity in the axial skeleton, re-study of *Birgeria stensioei* (PIMUZ T 4780) from the Middle Triassic of Monte San Giorgio revealed a slightly regionalized pattern, though the change in morphology is subtle compared with other taxa (Fig. 4; see Supplement Appendix S1 for details). In addition, the posterior vertebral column of the species *B. liui* from the Middle Triassic of China has recently been described (Ni *et al.*, 2019) and can be used for comparison.

Region I is characterized by short, robust, curved neural spines and stout supraneurals in PIMUZ T 15, T 2775 and T 4780.

Region II consists of at least 22 paired elements. The dorsal ossifications are relatively small, with a high neural arch, and short, thickened, caudally curved neural spines. Distally, the neural spines articulate with relatively robust supraneurals, which have a gently curved S-shape and a blunt distal end. Ventral ossifications, interpreted as parapophyses, are present. In some specimens, the parapophyses show a tuberosity, similar to structures that, in other *Birgeria* species, have been interpreted as attachment structures for cartilaginous ribs (*B. groenlandica*: Nielsen, 1949). This division agrees well with *Australosomus* (Fig. 5c; also see Nielsen, 1949).

In Region III, anterior processes on the neural arches are present and distinctive, and posterior processes are absent. Supraneurals are present. The supraneurals are straight or slightly curved, with their concave side facing anteriorly. Parapophyses are ossified, but ventral arcocentra are absent or cartilaginous in *B. stensioei*. Ossified plate-like ventral arcocentra fused to the parapophyses are present in Region III in *B. liui* (Ni *et al.*, 2019).

The transitional region has four parts: IVa is similar to III, but here spine-like haemal arches occur in addition to the parapophyses; these were interpreted as ribs in *B. liui* by Ni *et al.* (2019). Neural arches are paired and similar in morphology to those in Region III, and supraneurals are present. Region IVb is marked by the absence of ossified parapophyses, although some large plate-like ossifications preserved ex situ complicate interpretation (Fig. 4). The spine-like haemal arches gradually increase in length posteriorly. Supraneurals are present. In IVc, the haemal arches abruptly become broader and larger relative to those in IVb. Neural arches and spines are similar to those in more anterior subregions. In IVd, supraneurals are absent. The paired neural spines are more elongate and the haemal arches are broader than in more anterior subsections of Region IV.

Region V is characterized by median, unpaired neural and haemal spines. The long axes of the haemal arch and spine are offset, forming an angle in lateral view. This is similar to the anterior caudal region in *B. liui*.

Region VI is characterized by slender haemal arches that are not offset from the median haemal spines. Externally, scale cover begins in this region. Region VI in *B. stensioei* is characterized by a change in the inclination of the neural spines, similar to the posterior caudal region in *B. liui* (Ni *et al.*, 2019).

Regions VII + VIII support the lepidotrichia of the caudal fin. Haemal arches with a median hypural plate are present in Region VII; the condition of the dorsal ossifications is unclear due to scale cover. Haemal arches are absent in region VIII.

As in *Saurichthys rieppeli*, all eight regions can be recognized in *Birgeria*. Region IV in *Birgeria* also represents a transition between the abdominal and caudal axial skeleton, with a progressive loss of 'abdominal' phenotypes (e.g. parapophyses, supraneurals) and an acquisition of 'caudal' phenotypes (e.g. elongated, robust haemal processes that resemble haemal spines in all aspects except median fusion) over many axial segments. As in *S. rieppeli* and the Early Triassic saurichthyids, the boundary between the abdominal and transitional regions correlates with the position of the pelvic girdle.

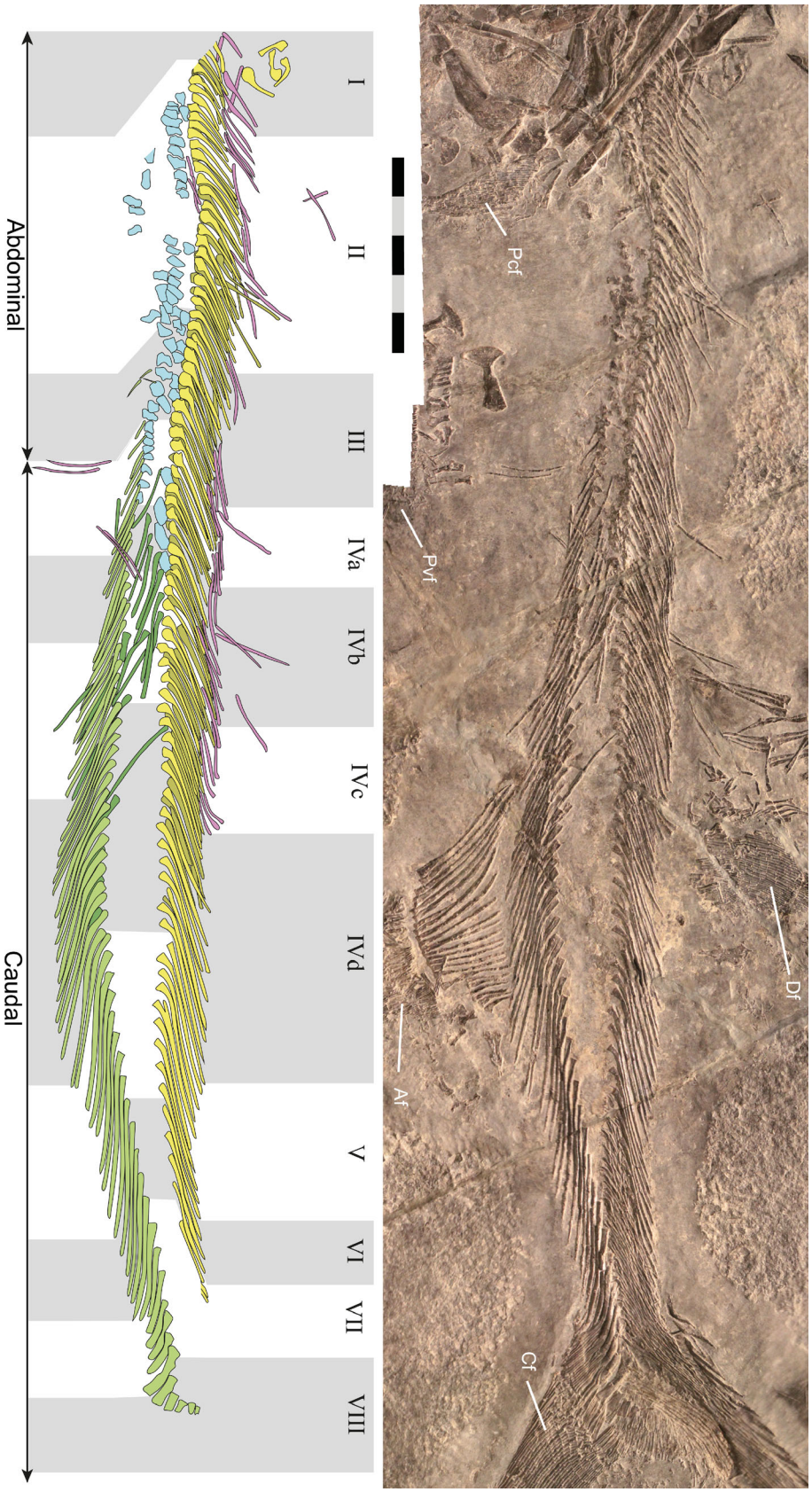
Abdominal
Caudal
I
II
III
IVa
IVb
IVc
IVd
V
VI
VII
VIII
Pcf
Pvf
Df
Af
Cf

Figure 4 The postcranial axial skeleton of *Birgeria stensioei* (PIMUZ T 4780; mirrored). Roman numerals indicate regions discussed in the text, and serially homologous structures are colour-coded: light yellow – right-hand neural arches/spines; greyish yellow – left-hand neural arches/spines; purple – supraneurals; light blue – parapophyses; light green – right-hand haemal processes/spines; dark green – left-hand haemal processes. Abbreviations: Af, anal fin; Cf, caudal fin; Df, dorsal fin; Pcf, pectoral fin; Pvf, pelvic fin. Scale bar = 5 cm.

Regionalization in outgroups: *Australosomus*

In contrast to *Birgeria* and Saurichthyidae, *Australosomus kochi* has ossified vertebral centra. All eight axial regions are differentiated in the latter taxon (Fig. 5c, Table S1; data from Nielsen, 1949). As in *Birgeria*, shorter, thicker neural spines characterize Regions I and II. A small lateral process on the ventral arcocentrum (parapophysis) suggests that vertebrae in the postoccipital region (I) may have borne cartilaginous ribs, unlike in teleosts (e.g. De Clercq *et al.*, 2017). The subregions of Region IV are not well-documented in *A. kochi*, but there is some evidence that loss of parapophyses, appearance of haemal spines, and fusion of neural arches and interdorsal elements do not occur simultaneously. Region V is characterized by diplospondyly, and Regions VI–VIII are similar to saurichthyids.

Discussion

Both axial regionalization and differentiation appear to have declined in Saurichthyidae over evolutionary time, with the highest number of and clearest differentiation between regions observed in basal species and outgroup taxa (Fig. 3). Loss of differentiation between the anterior- and mid-abdominal regions (Regions II–III) and between the caudal and peduncle regions (V–VI) evolved multiple times within the clade. Two groups of saurichthyids show independent decreases in regionalization (*Saurichthys grignae*, and the *Saurorhynchus* species group), affecting regions of both the abdominal and caudal vertebral column. In view of this within-group evolutionary lability, as well as the well-documented variation in vertebral regionalization across clades (see below and Table S1) we are not assuming direct homology between regions across Actinopterygii.

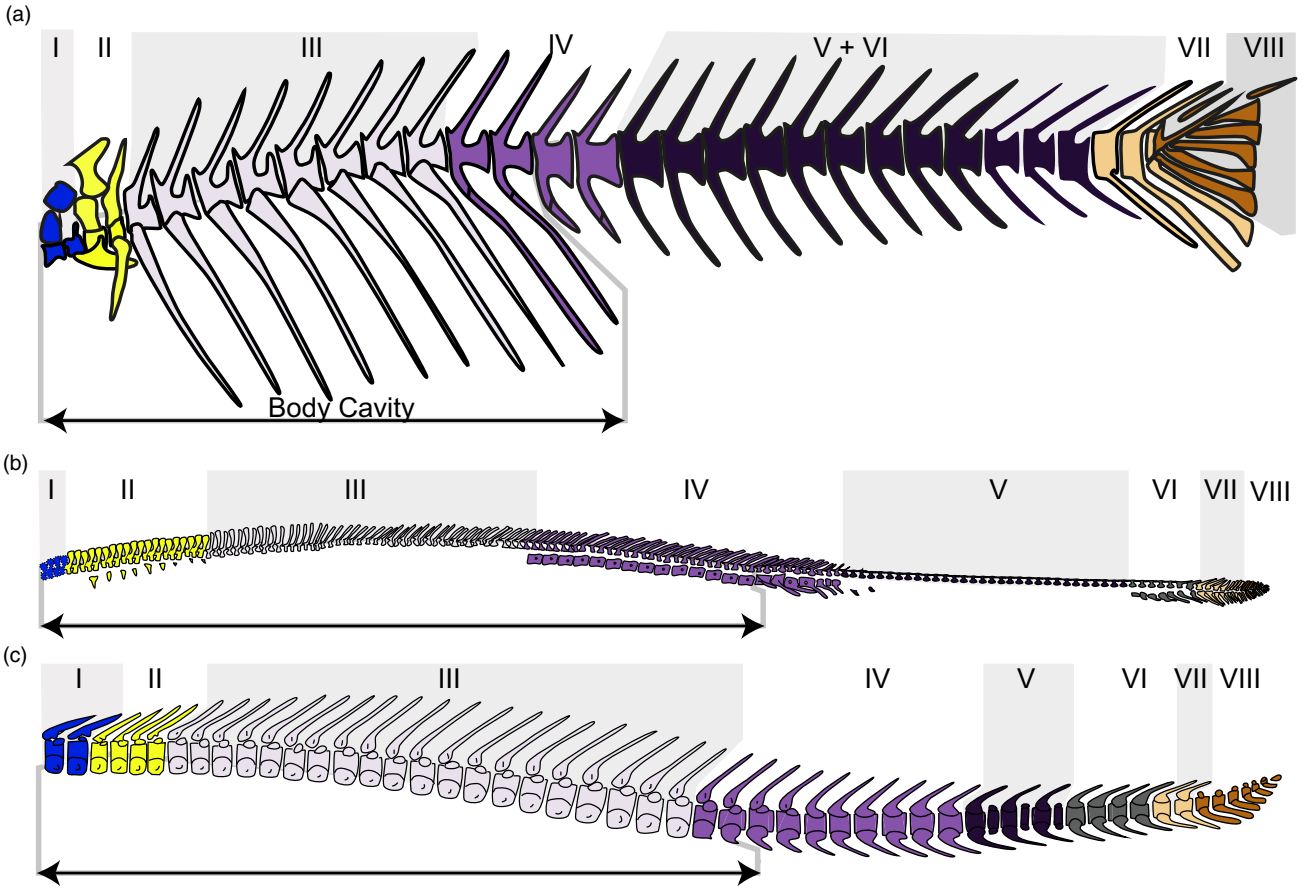

Figure 5 Comparison of axial regionalization in (a) *Danio rerio* (redrawn from Bird & Mabee (2003), modified based on Morin-Kensicki *et al.*, 2002; Sallan, 2012); (b) reconstructed axial skeleton of *Saurichthys rieppeli*; (c) reconstruction of the axial skeleton of *Australosomus kochi* (redrawn from Nielsen, 1949).

Rather, we are hypothesizing iterative evolution of differentiated axial regions based on a shared underlying developmental framework (deep homology). Such a view is consistent with reports of differentiation in various regions of the axial skeleton in jawless vertebrates (Chevrinais *et al*., 2018).

Axial regionalization across Actinopterygii

Two to three postoccipital (cervical) vertebrae, identified by the absence of ribs, are morphologically distinctive in both *Danio* and *Oncorhynchus*, and in *Danio* correspond to similar gene expression boundaries as the cervical region in tetrapods (Table 2; Morin-Kensicki *et al*., 2002; De Clercq *et al*., 2017). However, the absence of ribs in the postoccipital vertebrae is not universal in actinopterygians (e.g., *Lepisosteus*: Grande, 2010; *Australosomus*: Nielsen, 1949). The vertebrate neck is defined as the domain of the cucullaris muscle, which inserts on the pectoral girdle (Kuratani, 2008). Thus, patterning of the 'cervical' region is closely correlated with the position of the brachial plexus in all vertebrate groups (Burke *et al*., 1995). It seems likely that a short postoccipital region will be conserved across Actinopterygii, but incorporation of vertebrae into the back of the skull may complicate assessment of homologies (Grande & Bemis, 1998). Due to the high counts, the anteriormost well-preserved neural arches of *Saurichthys rieppeli* likely do not correspond to the postoccipital vertebrae.

The abdominal region in *Danio* consists of very few vertebrae, and the transition between the two posterior Weberian vertebrae and the abdominal region is patterned using the same genetic underpinnings as the thoracolumbar transition in amniotes (Morin-Kensicki *et al*., 2002). In the non-teleostean actinopterygians surveyed here, the abdominal region is elongated in comparison with *Danio*, but the anterior- and mid-abdominal regions are usually either very subtly differentiated or undifferentiated. This configuration is more similar to that described in chondrichthyans (Oulion *et al*., 2011), and may represent the primitive state in gnathostomes.

The widely recognized abdominal–caudal transition in actinopterygians, defined by the first occurrence of haemal spines/processes (e.g. Bird & Mabee, 2003), falls within a highly conserved zone in which abdominal and caudal vertebral morphologies overlap in the region of the posterior body cavity and anterior tail. This transitional region (Region IV; Type III of *De Clercq et al*., 2017) spans the abdominal–caudal boundary, and has even been reported in jawless vertebrates (*Euphanerops*; Chevrinais *et al*., 2018). This region coincides with the expression domain of Hox PG11 in chondrichthyans (Oulion *et al*., 2011), a sacral marker in tetrapods (Wellik, 2007). In *S. rieppeli*, the 'abdominal' portion of the transitional region (IVa) is particularly expanded relative to the outgroup taxon *Australosomus* (Fig. 5c), and some other saurichthyids (e.g. *Costasaurichthys* species group, see also Table S1). Interestingly, in *Birgeria*, the body cavity extends ventral to Region IVb (Fig. 4); thus although the transitional region is expanded in *Birgeria*, this has been achieved via a different mechanism than in *S. rieppeli*. Expansion of Region

Table 2 Tentative deep homologization of axial regions and terminology in actinopterygians. References: *Danio* (Morin-Kensicki *et al*., 2002; Bird& Mabee, 2003); *Oncorhynchus* (De Clercq *et al*., 2017); *Tarrasius* (Sallan, 2012); *Saurichthys rieppeli* (Maxwell *et al*., 2015; this study); Hox paralogous groups (PG; Burke *et al*., 1995; Wellik, 2007)

	'Cervical'	Thoracic	'Lumbar'	'Sacral'	Caudal	Peduncle	Preural	Ural
Danio Fig. 5a	Postcranial / Weberian /Cervical	Weberian	Abdominal	Variable	Caudal		Preural	Ural
Oncorhynchus	Type I	Type II		Type IIIa-d	Type IV		Type V	Type VI
Tarrasius	Not preserved	'Cervical'	Thoracic	Lumbar + sacral	Caudal	Not preserved	Not preserved	Not preserved
Saurichthys rieppeli Fig. 5b	Not preserved	Anterior abdominal (Region II)	Mid-abdominal (Region III)	Transitional (Region IVa-c)	Caudal (Region V)	Peduncle (Region VI)	Preural (Region VII)	Ural (Region VIII)
Hox PG		Hox PG6 (cervico-thoracic)	Hox PG9 (thoraco-lumbar)	Hox PG10 (lumbo-sacral)	Hox PG11 (sacro-caudal) + Hox PG12 (caudal)			

IV well into the abdominal region may promote axial stability (see below).

The anterior caudal region (V), beginning several segments posterior to the end of the body cavity, is widely conserved and has been described in *Tarrasius*, *Oncorhynchus*, and corresponds to the end of the 'variable' region (sensu Morin-Kensicki *et al*., 2002: fig. 6) in *Danio* (Table 2; Sallan, 2012, Bird& Mabee,2003; De Clercq *et al*., 2017; Morin-Kensicki *et al*., 2002). In *Saurichthys rieppeli*, this region is interpreted as beginning at the point where the neural spines disappear, although ossified haemal processes are absent in this species. The posterior caudal region of *S. rieppeli* is further differentiated, with three additional regions: the caudal peduncle (VI), and the preural and ural caudal fin regions (VII-VIII). Region VI is differentiated in *Australosomus* and *Birgeria*, as well as in basal saurichthyids, implying phylogenetic continuity in this part of the tree; however, Region VI is not widely conserved in actinopterygians (Table 2; Table S1). Convergent differentiation of this region has occurred in some teleosts (e.g. *Thunnus*, *Trachurus*: Clothier, 1950). The developmental basis for posterior axial regionalization is poorly understood: the caudal region, including the tail fin, is induced by an independent organizer (Agathon *et al*., 2003), and may be patterned separately from the rest of the axis (Morin-Kensicki *et al*., 2002). *Hox* genes may be involved but their role in conferring identity is not clear (Ahn & Gibson, 1999).

Functional interpretation

Taphonomic disarticulation is concentrated at particular points along the body in Middle Triassic saurichthyids (Beardmore & Furrer, 2016). In *Saurichthys curionii*, the anterior abdominal regions (II/III) and the region posterior to the median fins (Regions V–VI) were particularly affected by disarticulation, whereas in the *Costasaurichthys* species group, bending and disruption of the axial skeleton were concentrated anteriorly (II/III) and regions V–VII were rigid. In all cases, the region of the axial skeleton with elongated haemal processes (IVa/IVb) showed the least flexibility. This suggests bending during locomotion was concentrated anterior to Region IV in most species of *Saurichthys* (as reconstructed by Kogan *et al*., 2015), with additional posterior flexibility in the skeleton of *S. curionii* possibly associated with a more anguilliform swimming style. A regionally differentiated axial skeleton in a fully aquatic organism therefore might be adaptive in the control of bending and flexibility along the vertebral column associated with specialized locomotor strategies.

Conclusions

Differentiation of axial regions in bony fishes varies considerably even within clades in which a highly differentiated axial skeleton is the primitive condition (Saurichthyidae: this study). The axial skeleton of *Saurichthys rieppeli* shows a high level of regionalization, similar to that of the Carboniferous actinopterygian *Tarrasius* (Sallan, 2012), and all available evidence suggests that the capacity to generate morphologically disparate axial regions is conserved across Osteichthyes (Table 2). As with *Tarrasius*, regional differentiation in saurichthyids is not associated with a terrestrial or amphibious lifestyle, but may be associated with elongation of the abdominal region, as regional differentiation appears to exert differential control on flexibility and stability of the vertebral column. Whether these qualitative morphological regions correlate with the regions recovered using linear measurements and associated with swimming style in teleosts (Meunier & Ramzu, 2006) remains to be tested morphometrically.

The specific morphologies characterizing these axial regions and relative disparity between them is variably expressed in Actinopterygii (see Table S1). However, the developmental framework underpinning a regionalized vertebral column is likely to be conserved (Oulion *et al*., 2011). The probability of a conserved framework underlying superficially convergent axial morphologies in fishes opens up several interesting lines of investigation, such as the relationship between within-column disparity and evolutionary radiations, or meristic variation of specific regions in relation to body shape and axial flexibility across clades.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Regional differentiation across Actinopterygii: summary Table S1 and discussion of regionalization in *Birgeria, Lepisosteus and Amia*.

Table S1. Regional differentiation across Actinopterygii.